Soils of temperate rainforests of the North American Pacific Coast

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ABSTRACT

Temperate rainforests have high conservation and natural resource value, but the soils of this bioregion have not previously been studied as a unit. Here we examine the soils of North America's Pacific coastal temperate rainforests, utilizing databases from the United States Natural Resources Conservation Service and the Canadian Centre for Land and Biological Resources Research to (i) identify the soil taxa, (ii) evaluate the soil properties, and (iii) compare soils in temperate and tropical rainforests. There are strong climate gradients within these temperate rainforests, with the mean temperature declining from 11.7 °C to 6.1 °C and the mean annual precipitation increasing from 1500 mm to around 3000 mm from northern California (CA) to northwestern British Columbia (BC) and southeastern Alaska (AK). There is also high pedodiversity in this region, with soils representing 8 orders and 31 suborders, and, in the US portion, 65 great-groups, 142 subgroups, and 482 soil series. Twenty-six percent of described soil series are endemic to temperate rainforests in the US portion of the region, with the proportion declining with latitude. Dominant soil suborders vary along the latitudinal gradient from Humults–Udalfs/Ustalfs–Udepts–Udults in CA, to Udands–Udepts–Udands Humults in western Oregon (OR) and Washington (WA), to Orthods–Folists in BC and Cryods–Saprists in AK. The dominant diagnostic horizons are ochric/argillic (CA), umbric/cambic (OR, WA), and albic–histic/spodic (BC, AK). Whereas soils in CA, BC, and AK tend to have a mixed mineralogy, those in northern OR and WA commonly are derived from volcaniclastic materials and have a ferrihydritic or isotic mineralogy. Soils in this region are generally deep, hold abundant moisture, are not subject to deep-freezing, and are enriched in extractable Fe and Al. Organic C and total N contents are high overall, but also variable, with right-skewed distributions. Compared to tropical rainforest soils in the Pacific Basin, Pacific temperate rainforest have greater weatherable minerals, cation-exchange capacities, soil organic C, and total exchangeable base cations. However, soils of both bioregions tend to be deep, acidic Al-saturated, and can have large N reservoirs. This investigation provides a foundation for a more unified understanding of the soils of a globally significant bioregion.

1. Introduction

Temperate rainforests have not received th`e same attention as their tropical counterparts, and though they make up only about 2% of the world's forests, they hold high value for both conservation and natural resources (DellaSala et al., 2011). These forests, sometimes called wet temperate forests, have been defined in several ways. Alaback (1991) laid out four parameters, later refined by Kellogg (1992): (i) greater than 1400 mm of annual precipitation, with at least 10% occurring during the summer; (ii) cool, frequently overcast summers, with a July (or austral January) isotherm of <l6 °C; (iii) infrequent fires; and (iv) a dormant season caused by low temperatures, potentially accompanied by transient snow. For conservation purposes, DellaSala et al. (2011) built upon this definition and constructed a rainforest climate model that acknowledged rainforests in boreal regions and highlighted several outlier regions of previously less-recognized rainforests. Worldwide, temperate rainforests occupy over 400,000 km^2, and well over 1 million km^2 by some estimates and definitions (Table 1). The largest areas occur in northwestern North America and southwestern South America, with substantial areas also found in East Asia, Australasia, and western Eurasia.

Temperate rainforests, like their tropical counterparts, are highly productive and also contain some of the highest densities of biomass of any terrestrial ecosystem (Keith et al., 2009; Waring and Franklin, 1979). Soils in tropical rainforests are commonly Oxisols and Ultisols, which generally have low levels of nutrients and weatherable minerals (Coscione et al., 2005; Padmanabhan et al., 2012). To mitigate against the poor soil conditions, tropical rainforests have adapted special mechanisms to cycle nutrients more directly from the plant to the rooting zone (Stark and Jordan, 1978). Soils of temperate rainforests have not been studied as comprehensively as those of tropical rainforests. Maintaining the productivity of temperate rainforests to meet increasing

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Table 1
Global distribution of temperate rainforests.
Area estimates are compiled from Kellogg (1992) and DellaSala et al. (2011).

Region	Location(s)	Area estimates [km^2]
Northwestern North America	All	207,000–320,000
	Pacific Coast	207,000–273,000
	Inland Northwest	0–72,000
South America	Chile, southwestern Argentina	120,000–126,000
Australasia	Tasmania, New Zealand, eastern Australia	46,000–86,000
East Asia	Japan, Korea, eastern Russian	24,000–151,000
Western Eurasia	Caucasus, Alps, British Isles (relicts)	39,000–180,000
Others	Eastern North America, South Africa, Himalayas	0–100,000+
Total		436,000–1,308,000+
This study	North American Pacific Coast, excluding Cascades and Coast Mountains	166,331

human demands requires a complete understanding of these ecosystems, including their soils (Kimmins, 1996). Based on a few studies, these soils appear to be moderately weathered (Bockheim et al., 1996; Burt and Alexander, 1996; Hedin et al., 1995; Heilman and Gass, 1974) and enriched in soil organic carbon and nitrogen (Edmonds and Chappell, 1994; Huygens et al., 2008; Perakis and Sinkhorn, 2011; Smithwick et al., 2002). Most temperate rainforests occur near oceans that help maintain a mild climate conducive to a long growing season, evergreen vegetation, and slow rates of decomposition (Lawford et al., 1995; Waring and Franklin, 1979). Abundant precipitation can lead to rapid leaching (Burt and Alexander, 1996; Langley-Turnbaugh and Bockheim, 1998; Ugolini, 1968). Marine inputs appear to be important in the nutrition of these ecosystems and their soils (Bockheim and Langley-Turnbaugh, 1997; Gende et al., 2002). Diverse topography and histories of glaciation and volcanism in many temperate rainforest regions contribute to a variety of parent materials and weathering processes (Alexander and Burt, 1996; Bockheim et al., 1996; Briggs et al., 2006).

Given this particular combination of pedogenic factors, what sorts of soils are found in temperate rainforests, and how does this help us understand the ecosystems in this bioregion? To our knowledge, no one has yet investigated the characteristics of temperate rainforest soils as a unit. The objectives of this study are to delineate the soils in North America's Pacific coastal temperate rainforests, evaluate their properties, and discuss their role in rainforest ecosystems in comparison with their tropical counterparts. We utilize data from the US and Canadian soil databases and draw from a wide range of published literature to synthesize our knowledge of temperate rainforest soils of North America's Pacific Coast.

2. Coastal temperate rainforests of the North American Pacific Coast

2.1. Study area

We focus on the soils of the rainforests of North America's Pacific Coast (NAPC). This region, sometimes referred to as the Pacific Northwest, spans much of the west coast of the US and Canada, up to about 85 km inland. Though rainforests exist further inland (e.g. in the western Cascade mountains), there is less consensus over their delineation (DellaSala et al., 2011), and we decided to limit our study to the most quintessential rainforests on the coast. The study region consists of the Coast Range and Coastal Western Hemlock–Sitka Spruce Forest ecoregions (Level III), as defined by the North American Commission on Environmental Cooperation (Wiken et al., 2011; Fig. 1). Within the study region, soils have been divided into ecological units — Major Land Resource Areas (MLRAs; Natural Resource Conservation Service, 2006) in the US and Ecoregions in Canada (Demarchi, 2011; Ecological Stratification Working Group, 1996; Fig. 1). The US subregions include

Fig. 1. The coastal temperate rainforests of western North America and subregions.

the Northern Coast Range and Sitka Spruce Belt (MLRA 1 and 4A) in western Oregon (OR) and Washington (WA), the Coastal Redwood Belt (MLRA 4B) in northern California (CA), and the Gulf of Alaska Coast (MLRA 220) in southeastern Alaska (AK). The Canadian subregions are all in the coastal British Columbia (BC), and include Western Vancouver Island (Ecoregion 193), Gwaii Haanas (Ecoregions 188 and 189; formerly Queen Charlotte Ranges and Lowlands), and the portion of the Coastal Gap (Ecoregion 191) falling inside the larger study region boundaries.

2.2. Climate

The climate of NAPC rainforests has been described in detail elsewhere (e.g. Lawford et al., 1995), but can be generally characterized as mild-temperate mesothermal (Köppen Group C), with warm summers that range from dry in the south (Köppen Csb) to humid in the north (Köppen Cfb). Annual precipitation ranges from an average of 1500 mm in the Coastal Redwood Belt to 3300 mm in the Coastal Gap ecoregion (Table 2). Snow becomes more frequent with increasing latitude, accounting for less than 10% of precipitation in the south, but over 50% in the north. Mean annual air temperature decreases with latitude from 11.7 °C in the Coastal Redwood Belt to 6.1 °C along the Gulf of Alaska Coast (Table 2).

2.3. Vegetation

Vegetation in NAPC rainforests is dominated by about a dozen species of long-lived conifers, along with a few deciduous hardwoods, some less-common conifers, and a great diversity of understory plants. Most trees in the region have potential lifespans of over 400 years, with some able to live well over 1000 years (Waring and Franklin, 1979). Aboveground biomass in temperate rainforests of the NAPC ranges from 300 to 1000 Mg/ha, productivity from 5 to >15 Mg/ha/yr, and tree species richness from 2 to 20 (DellaSala et al., 2011; Hudiburg et al., 2009; Waring and Franklin, 1979). Disturbances include localized windthrow, landslides, and flooding; large, stand-replacing disturbances (e.g. fire) are uncommon, allowing succession to old-growth stages dominated by gap-phase dynamics.

Trees in the Coastal Redwood Belt include coastal redwood (*Sequoia sempervirons*), Douglas-fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), bishop pine (*Pinus muricata*), western red cedar (*Thuja plicata*), Sitka spruce (*Picea sitchensis*), Port Orford cedar (*Chamaecyparis lawsoniana*), red alder (*Alnus rubra*), California bay laurel (*Umbellularia californica*), golden chinkapin (*Castanoptis chrysophylla*), Pacific madrone (*Arbutus menziesii*), tanoak (*Notholithocarpus densiflorus*), and California black oak (*Quercus kelloggii*). Important understory species are red huckleberry (*Vaccinium parvifolium*), California huckleberry (*Vaccinium ovatum*), western swordfern (*Polystichum munitum*), wood-sorel (*Oxalis* spp.), *Trillium* spp., and *Rhododendron* spp. The Sitka Spruce Belt and Northern Pacific Coast Range forests contain Sitka spruce, western hemlock (*Tsuga heterophylla*), western red cedar, red alder, and Douglas-fir, along with lesser amounts of grand fir (*A. grandis*), bigleaf maple (*Acer macrophyllum*), and, at higher elevations, noble fir (*Abies procera*). The understory contains salal (*Gaultheria shallon*), swordfern, red huckleberry, wood sorel, *Rhododendron* spp., Oregon-grape (*Mahonia aquifolium*), *Rubus* spp., violets (*Viola* spp.), and *Trillium* spp. Forests in coastal BC (Western Vancouver Island, Gwaii Haanas, and Coastal Gap ecoregions) and the Gulf of Alaska Coast contain western hemlock, Sitka spruce, western red cedar, alder (*Alnus* spp.), Pacific Silver fir (*Abies amabalis*), shore pine (*Pinus contorta* subsp. *contorta*), mountain hemlock (*Tsuga mertensiana*), and Alaska yellow-cedar (*Chamaecyparis nootkatensis*). Common understory plants include step moss (*Hylocomium splendens*), salal, deer fern (*Blechnum spicant*), and Alaskan blueberry (*Vaccinium alaskaense*).

2.4. Physiography and soils

The physiography of the region is dominated by the Pacific Coast Ranges. In addition to isolated headlands, the landforms include uplifted marine terraces, sand dunes, river valleys cut through the mountains, and from northwest WA northward, glaciated terrain and colluvial fans. The soil parent materials include residuum, colluvium, marine deposits, alluvium, till, and volcanic ash. The latter deposits are most common in WA and southeast AK but occur throughout the area. Slopes commonly range between 0 and 90% and elevations from 0 to 2200 m above sea level (Natural Resource Conservation Service, 2006). The Natural Resource Conservation Service (2006) and Jungen and Lewis (1978) provide further discussion of physiography in the region.

According to the general soil maps of the USA (Soil Survey Staff, 2013a) and Canada (Centre for Land and Biological Resources Research, 1996), the dominant soil orders (suborders) in the western North America temperate rainforest are Alfisols (Ustalfs, Udalfs), Inceptisols (Udepts), and Ultisols (Udults) in northern CA, Inceptisols (Udepts) and Spodosols (Orthods) in OR, Andisols (Udands) in WA, Spodosols (Cryods/Ferro-Humic Podzols) and Histosols (Folists/Folisols) in BC, and Spodosols (Cryods) and Histosols (Saprists) in southeastern AK.

3. Methods

In the US portion of the study region, we identified dominant soil series within each subregion (MLRA) using the Natural Resource Conservation Service soil classification database (Soil Survey Staff, 2013b). A 50% cutoff was used to consider a soil series “dominant” in given county. Soil taxonomic features (to family level), site factors (e.g. climate, parent materials), general soil characteristics (e.g. soil depth, drainage class, temperature and moisture regime), and diagnostic horizons were determined from Official Soil Series Descriptions (Soil Survey Staff, 2013c). The Soil Survey Geographic (SSURGO) Database (Soil Survey Staff, 2012) was used to generate soil maps for each MLRA. Extraction of soil map data was accomplished using a vector database of MLRAs (Natural Resource Conservation Service, 2006). Each SSURGO map unit is made up of component soils. The component with the highest percent coverage was selected as the dominant component for soil map preparation.

Soil property characterization data were obtained from Soil Laboratory Data (National Cooperative Soil Survey, 2013) for available and randomly selected soil series for major soil taxa. We used the laboratory data to calculate profile average pH, cation exchange capacity (CEC), Al saturation and base saturation, as well as profile (to 100 cm) quantities of soil organic C, total N, exchangeable bases (Ca, Mg, Na, and K), and C:N ratio, based on bulk density and stone content. Missing bulk density values were estimated using the pedotransfer functions of Heuscher et al. (2005) where feasible (~31% of horizons), and additional missing data (bulk density (~8% of horizons), coarse fragments (~38% of horizons), and total N (~14% of horizons)) were estimated from comparable pedons and horizons where reasonable (see Supplement S1). We calculated summary statistics for analytic properties across all soil profiles and compare them with other local and global sources. A number of the properties examined have right-skewed distributions, so in addition to reporting mean (MN), minimum, and maximum values, we also report median (MD) and interquartile range (IQR; i.e. 25th–75th percentiles), which are more robust to outliers and skewed distributions.

The BC portion of the study region is largely outside the agricultural zone of Canada where detailed soil property and taxonomic data are available. Extensive soil spatial data exists only at a relatively coarse scale of 1:1 million. To identify and map BC soil taxa and characteristics, we used the Soil Landscapes of Canada database (Centre for Land and Biological Resources Research, 1996), Soil Landscapes of BC descriptions (Jungen and Lewis, 1978) and the Canadian guide to soil classification (Soil Classification Working Group, 1998). Mapping in BC was similarly

Table 2
Regional comparison of soil characteristics and forming factors in coastal temperate rainforests of western North America. Sources for the U.S. subregions were Soil Survey Staff (2013b, 2013c) and for the Canadian subregions were Centre for Land and Biological Resources Research (1996), Jungen and Lewis (1978) and Soil Classification Working Group (1998).

Subregion	Coastal Redwood Belt (MLRA 4B)	Sitka Spruce Belt (MLRA 4A)	Northern Pacific Coast Range (MLRA 1)	Western Vancouver Island (Ecoregion 193)	Coastal Gap (Ecoregion 191)	Gwaii Haanas (Ecoregions 188 & 189)	Gulf of Alaska Coast (MLRA 220)
Total area (area of mapped soil series) [km^2]	12,095 (4550)	13,740 (10,440)	26,675 (23,481)	20,088 (na)	15,455 (na)	10,193 (na)	71,085 (17,732)
Mean annual air temperature [°C]	11.7	9.4	8.9	8.5	7.5	8.0	6.1
Mean annual precipitation [mm]	1500	2500	2300	3000	3300	1800	2600
No. of soil series	63	173	214	nd	nd	nd	32
Ranking soil orders	Ultisols (41%), Alfisols (21%), Inceptisols (19%)	Andisols (49%), Inceptisols (30%), Ultisols (9%)	Inceptisols (43%), Andisols (31%), Ultisols (15%)	Podzolic/Spodosols (85%)	Podzolic/Spodosols (50%), Organic/Histosols (48%)	Podzolic/Spodosols (83%), Organic/Histosols (16%)	Spodosols (56%), Histosols (19%)
Dominant parent materials	Residuum & colluvium (75%)	Colluvium (29%), alluvium (23%), residuum (16%)	Colluvium & residuum (49%), colluvium (20%), alluvium (14%)	Colluvium (62%), till (18%)	Colluvium (44%), organic (40%)	Till (57%), colluvium (27%)	Colluvium, residuum (50%), organic (19%)
Depth	Deep	Deep	Deep	Shallow to moderately deep	Shallow to moderately deep	Shallow to moderately deep	Shallow to moderately deep
Drainage class	Moderately well to well	Moderately well	Moderately well to well	Moderately well to well	Well	Moderately well to well	Moderately well
Mineral class	Mixed (90%)	Ferrihydritic (41%), isotic (34%), mixed (23%)	Isotic (45%), ferrihydritic (28%), mixed (21%)	Mixed	Mixed	Mixed	mixed (100%)
Soil–temperature regime	Isomesic	Isomesic (80%), isofrigid (19%)	Mesic (70%), cryic or frigid (30%)	Isomesic, isofrigid, cryic	Isomesic, isofrigid, cryic	Isomesic, isofrigid, cryic	Cryic
Soil–moisture regime	Udic (65%), ustic (17%)	Udic (84%), aquic (16%)	Udic (89%)	Udic, aquic	Udic, aquic	Udic, aquic	Udic (66%), aquic (34%)
Particle–size class	Fine–loamy (41%), fine (25%), loamy-skeletal (16%)	Medial or medial–skeletal (48%), fine (16%), fine-loamy (10%)	Medial or medial–skeletal (30%), loamy–skeletal (21%), fine (17%)	Loamy–skeletal, sandy–skeletal	Loamy–skeletal, sandy–skeletal, organic	Loamy–skeletal, sandy–skeletal	Loamy–skeletal (53%), organic (19%)
Cation-exchange activity class	Superactive (43%), semi-active (19%), active (22%)	None (89%), superactive (9%)	None (82%), superactive (10%)	None, superactive	None, superactive	None, superactive	Superactive (66%)
Dominant diagnostic epipedon	Ochric (73%)	Umbric (60%), ochric (27%)	Ochric (52%), umbric (42%)	None	Organic	Organic	Histic (34%), albic (47%)
Epipedon thickness [cm]	33	38	30	–	Usually ≥40	Usually ≥40	20
Dominant diagnostic subsurface horizon	Argillic (71%)	Cambic (74%), none (10%)	Cambic (76%), argillic (22%)	Podzolic	Podzolic	Podzolic	Spodic (56%)
Subsurface diagn. hor. thickness [cm]	91	69	71	≥10	≥10	≥10	23

Table 3a
Soil taxa in coastal temperate rainforests of the western United States. Number of soil series in each subgroup indicated in parentheses.
Data from Soil Survey Staff (2013b, 2013c).

Order	Suborder	Great group	Subgroup	Area [km^2]
Alfisols	Aqualfs	Endoaqualfs	Umbric (1)	17
		Glossaqualfs	Typic (1)	195
	Udalfs	Glossudalfs	Oxyaquic (3), Oxyaquic Vertic (2)	77
		Hapludalfs	Aquultic (1), Mollic (2), Oxyaquic (1), Ultic (8)	928
	Ustalfs	Haplustalfs	Ultic (4)	1326
	Xeralfs	Haploxeralfs	Aquultic (1)	7
		Palexeralfs	Aquic (1), Ultic (1)	521
	Subtotal			3071
Andisols	Aquands	Duraquands	Typic (1)	17
		Endoaquands	Alic (1)	5
		Epiaquands	Alic (3)	31
		Melanaquands	Typic (4)	3
	Cryands	Fulvicryands	Pachic (1), Typic (3)	48
		Haplocryands	Alic (1), Typic (1)	208
	Udands	Durudands	Aquic (3), Typic (4)	477
		Fulvudands	Aquic (7), Eutric Pachic (5), Lithic (3), Oxyaquic (3), Pachic (19), Typic (40)	8020
		Hapludands	Alic (17), Aquic (1), Lithic (3), Oxyaquic (2), Typic (13), Vitric (3)	3122
		Melanudands	Typic (1)	392
	Subtotal			12,353
Entisols	Aquents	Cryaquents	Typic (1)	19
		Fulvaquents	Aeric (1), Typic (1)	35
	Fluvents	Cryofluvents	Typic (1)	362
		Udifluvents	Oxyaquic (1), Typic (4), Vitrandic (1)	197
	Orthents	Cryorthents	Lithic (1), Typic (1)	30
	Psamments	Udipsamments	Typic (3)	133
	Subtotal			776
Histosols	Folists	Cryofolists	Lithic (1)	1811
	Hemists	Haplohemists	Terric (2)	30
	Saprists	Cryosaprists	Lithic (3), Terric (1), Typic (1)	3888
		Haplosaprists	Hemic (1)	43
	Subtotal			5772
Inceptisols	Aquepts	Cryaquepts	Aeric (1), Histic (1), Histic Lithic (1)	68
		Endoaquepts	Fluvaquentic (3), Vertic (4)	308
		Epiaquepts	Aeric (1)	25
		Humaquepts	Aeric (1), Aquandic (1), Fluvaquentic (2), Typic (6)	227
		Petraquepts	Histic Placic (1), Typic (1)	116
	Cryepts	Dystrocryepts	Andic (2), Lithic (1)	40
		Eutrucryepts	Humic (1)	73
	Udepts	Dystrudepts	Andic (9), Andic Oxyaquic (4), Aquandic (3), Humic (19), Lithic (3), Oxyaquic (2), Typic (13)	3042
		Eutrudepts	Aquertic (1), Dystric (8), Lithic (3)	1872
		Fragiudepts	Andic (1), Typic (1)	292
		Humudepts	Andic (21), Andic Oxyaquic (1), Aquandic (3), Aquic (1), Cumulic (1), Fluventic (3), Lithic (2), Oxyaquic (2), Pachic (5), Psammentic (1), Typic (16)	8739
	Ustepts	Dystrustepts	Humic (1), Lithic (1), Typic (1)	35
		Humustepts	Typic (1)	25
	Xerepts	Dystroxerepts	Andic (3), Aquic (1), Typic (1), Vitrandic (1)	1003
	Subtotal			15,869
Mollisols	Aquolls	Endoaquolls	Cumulic (1), Fluvaquentic (2)	29
		Epiaquolls	Typic (1)	1
	Udolls	Argiudolls	Aquic (2), Typic (2)	21
		Hapludolls	Typic (1)	8
	Xerolls	Argiustolls	Pachic (1)	6
		Argixerolls	Pachic Ultic (1), Ultic (1)	203
		Haploxerolls	Cumulic Ultic (1), Lithic Ultic (1), Pachic Ultic (1), Ultic (1)	181
	Subtotal			449
Spodosols	Aquods	Cryaquods	Lithic (1), Typic (1)	1789
		Duraquods	Typic (3)	55
		Endoaquods	Typic (1)	58
		Epiaquods	Typic (1)	5
	Cryods	Haplocryods	Typic (1)	11
		Humicryods	Lithic (5), Typic (9)	9660
	Orthods	Durorthods	Typic (1)	40
		Haplorthods	Aquic (1), Entic (1), Oxyaquic (1), Typic (4)	253
	Subtotal			11,871
Ultisols	Aquults	Albaquults	Typic (1)	4
		Paleaquults	Umbric (1)	20
		Umbraquults	Typic (2)	12
	Humults	Haplohumults	Andic (2), Aquic (1), Oxyaquic (2), Plinthic (1), Typic (25)	2415
		Kandihumults	Typic (2)	40
		Palehumults	Andic (1), Aquic (2), Oxyaquic (2), Typic (20), Xeric (3)	3196
	Udults	Hapludults	Aquic (1), Lithic (1), Typic (3)	97
		Paleudults	Typic (1)	78
	Ustalts	Haplustults	Typic (2)	144
	Subtotal			5862
Total: 8	30	66	142 (482)	55,989

Table 3b
Soil taxa in coastal temperate rainforests of British Columbia, Canada. Data from BC Ministry of Environment (2013) and Centre for Land and Biological Resources Research (1996). Taxa are listed using the Canadian System of Soil Classification terminology, followed by approximate Soil Taxonomy equivalent for order and great groups. Number of unlisted sub-taxa appears in parentheses.

Order	Great group	Subgroup	Area [km^2]
Podzolic/Spodosols	Humo-Ferric Podzols/Orthods	Duric, Gleyed Ortstein, Orthic, Ortstein, Placic	1700
	Ferro-Humic Podzols/Cryods	Duric, Gleyed, Gleyed Ortstein, Orthic, Ortstein, Placic	31,500
Organic/ Histosols	Fibrisols/Fibrists	Typic	170
	Humisols/Hemists	Terric, Typic	1250
	Mesisols/Saprists	Fibric, Terric, Typic	1400
	Folisols/Folists	Humic, Typic	7900
Gleysolic/ aquic suborders	–	–	400
	Gleysols/aquic suborders	Orthic, Rego	–
	Humic Gleysols/ aquic suborders	Orthic, Rego	–
Others (3)	Dystric Brunisols/ Dystrocryepts (5), Sombric Brunisol/ Cryepts (1), Regosol/Entisols (3), Gray Luvisols/Udalfs (1)	–	<100 each
Total: 6	12	33	44,300

based on the most dominant component in a mapping unit, with dominance determined as the highest areal percentage component within vector landscape units.

To compare soils of the temperate rainforests of western North America with those of tropical rainforests, we summarized data for soil series in the Perox suborder from Micronesia in the Pacific Basin (National Cooperative Soil Survey, 2013; Soil Survey Staff, 2013b, 2013c). The Perox suborder was selected for comparison because the seasonal distribution of precipitation approximates that of temperate rainforests in the NAPC region.

4. Results

4.1. Distribution of soil taxa

Soils of the western North American temperate rainforest are represented by 8 orders and 31 suborders (or Canadian great groups; Tables 3a and b). In the US portion of the region, there are 65 great groups and 142 subgroups (Table 3a), while in BC 33 Canadian subgroups have been identified (Table 3b). In the US databases there are 482 mapped soil series, accounting for 45% of the US portion and 33% of the entire study area, which we show here at the level of suborder (Fig. 2a and b).

Sixty-two of the 482 mapped soil series occur in the northwestern CA portion of the temperate rainforest, accounting for an area of 4550 km^2 (38% of MLRA 4B; Table 2). The soils are dominantly Ultisols (41% of mapped soil area), followed by Alfisols (22%), and Inceptisols (19%; Fig. 2a). Coastal OR and WA contain 387 soil series that account for 33,921 km^2 (84% of MLRAs 1 and 4A), including Andisols (40% of mapped soil area), Inceptisols (37%), and Ultisols (12%; Table 2; Fig. 2a). Soils in the BC rainforests are mapped to suborder (or Canadian great group; Fig. 2b). Western Vancouver Island is dominated by Podzolic soils (i.e. Spodosols; 85%), while the Coastal Gap ecoregion contains both Podzols (50%) and Organic soils (i.e. Histosols; 48%), as does Gwaii Haanas (83% and 16% respectively; Table 2). Only a small portion of the Gulf of Alaska Coast (MLRA 220) has been mapped, with 24 soil series recognized to date accounting for 17,732 km^2 (25% of the total area; Table 2; Fig. 2c). Five soil subgroups comprise 53% of the total mapped area of the US temperate rainforests: Typic Humicryods (5180 km^2), Lithic Humicryods (4129 km^2), Typic Fulvudands (4098 km^2), Terric Cryosaprists (1963 km^2), and Lithic Cryosaprists (1864 km^2).

4.2. Soil characteristics

Temperate rainforest soils in CA, OR and WA are deep (100–150 cm) to very deep (>150 cm) in terms of potential rooting, while those in coastal BC and southeastern AK are moderately deep (50–100 cm; Table 2). While there is considerable variation in drainage class within an MLRA, overall, the soils tend to be moderately well-drained to well-drained. The dominant soil–temperature regime varies with latitude, being isomesic (mean annual soil temperature at 50 cm ranges between 8 and 15 °C and the difference between the mean summer and winter temperature is <6 °C) in the Sitka Spruce and Coastal Redwood Belts (MLRAs 4B and 4A), mesic in the Northern Pacific Coast Range, isomesic to isofrigid or cryic in coastal BC, and cryic (mean annual soil temperature ranges between 0 and 8 °C without permafrost) along the Gulf of Alaska Coast. The dominant soil moisture regime is udic (no sustained period of drought), with an aquic regime also found in most subregions.

Soils in NAPC rainforests tend to occur in the finer particle-size classes, but often have abundant coarse fragments (Table 2). In CA the soils are mostly fine-loamy or loamy, while in OR and WA they are most commonly medial or medial–skeletal (volcanically derived soils with >35% coarse fragments). In coastal BC and southeast AK soils tend to fall into the organic or loamy– to sandy–skeletal size classes. Whereas soils in coastal CA, BC and AK often have a mixed mineralogy, those in western OR and WA are derived from volcanic materials and commonly have a ferrihydritic (abundant amorphous and organic-bound Fe) or isotic (abundant allophane) mineralogy. Although 43% of the soil series in temperate rainforests of northern CA are superactive (i.e., the ratio of the cation-exchange capacity (CEC) as determined from pH 7 ammonium acetate to clay is ≥0.6), soils elsewhere in the temperate rainforest of western North America contain less active clays.

The most common diagnostic surface and subsurface horizons in soils of the CA temperate rainforest are ochric and argillic, which average 33 and 91 cm in thickness, respectively (Table 2). Umbric or ochric and cambic horizons are most common in western OR and WA, averaging 30 to 38 and 67 to 71 cm, respectively. In coastal BC and AK, histic and spodic horizons are most common and average more than >20 cm and >10 cm in thickness, respectively (Table 2). Fig. 3 shows examples of coastal temperate rainforest soils, including a sandy, mixed, isomesic, ortstein, shallow Typic Duraquods (Blacklock soil series) from coastal Oregon, a fine, mixed, superactive, isomesic Typic Palehumults (Cunniff soil series) from coastal Oregon, a Humo-Ferric Podzol (Haplorthods) from coastal British Columbia, and a Lithic Humicryods from Port Graham, Alaska.

4.3. Soil analytic properties

We assembled analytical data for 27 soil series that are representative of the land area and taxonomic classes of soils in coastal temperate rainforests of western North America (Table 4, Fig. S1). Where possible these data were evaluated in comparison with values reported in the global datasets of Batjes (1997) and Post et al. (1985). Soils in NAPC rainforests tend to be moderately deep (MN: 122 cm, IQR: 86–150 cm) with bulk densities that are comparatively low overall (MN: 1.18 g/cm^3), but range widely (IQR: 0.91–1.42 g/cm^3) with extremes of 0.40 and 1.60 g/cm^3, the higher values from soils with ortstein horizons. These soils have fairly high CEC (MD: 33.1 $cmol_c/kg$, IQR: 16.9–41.2), but low effective CEC, base saturation (MD: 7%, IQR: 3–30), exchangeable cation concentration (MN: 2.3 $cmol_c/kg$, IQR: 1.5–4.8) and pH (MN: 5.0, IQR: 4.6–5.3; Table 4). Soils in this region can be Al-saturated (MN: 54%, IQR: 32–78) and are commonly enriched in extractable Fe and Al.

Profile quantities (to 100 cm) of SOC, total N, and exchangeable cations all exhibit right-skewed distributions in NAPC rainforests with a small number of very high values (Fig. 4; Table 4). Exchangeable base cation storage was mostly clustered around the median of 165 $kmol_c$/ha (IQR: 89–315 $kmol_c$/ha), but had a wide range, with two extremely high values (1256 and 2035 $kmol_c$/ha) indicating a particularly skewed distribution. SOC storage is variable (IQR: 116–439 Mg/ha), but generally high, with a median of 211 Mg C/ha. Storage of total N follows a similar pattern as SOC, with large variability (IQR: 7384–26,013) and a high median of 15,113 kg/ha, but with more large values. The highest SOC and total N values came from the same pedons, a Lithic Cryosaprist near Ketchikan, AK (1050 Mg C/ha, 44,385 kg N/ha), and a Typic Fulvudand near Grays Harbor, WA (763 Mg C/ha, 39,241 kg N/ha). C to N ratios were more normally distributed, with a fairly high mean of 18.4 and an interquartile range between 13.8 and 21.2.

5. Discussion

5.1. Pedodiversity

A key finding of this study is that the soils of NAPC temperate rainforests are exceedingly diverse. In the US, Pacific coastal rainforests contain 8 orders, 30 suborders, 65 great groups, and 142 subgroups, in addition to 482 soil series (Table 3a); coastal BC contains 6 Canadian soil orders, 12 great groups and 33 subgroups (Table 3b). Using the soil taxa richness–area relationships found by Guo et al. (2003), one would predict 7 orders, 17 suborders, 43 great groups, 125 subgroups, and 386 series in the US portion of our study region. The consistently greater number of taxa that we found means that at least in terms of soil taxa richness, NAPC rainforests have higher than expected pedodiversity. Guo et al. (2003) found that the western US as a whole has among the highest pedodiversities across a number of taxonomic scales, compared to other regions of the country. Using coarse climate

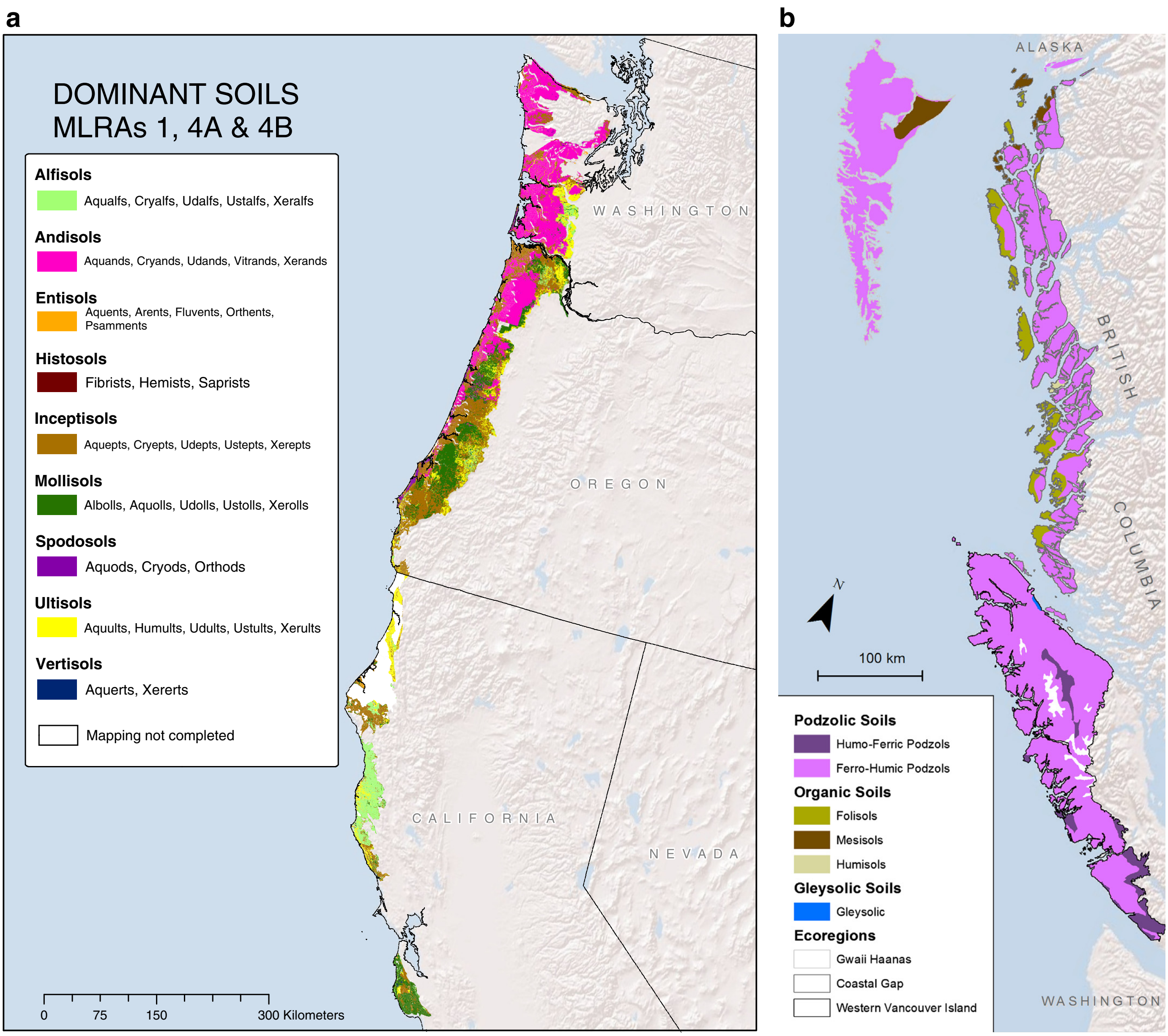

Fig. 2. a. Soil suborders in the Coastal Redwood Belt, Sitka Spruce Belt and Northern Pacific Coast Range subregions of the coastal temperate rainforest of western North America. Data from Soil Survey Staff (2012). b. Soil great groups (US suborders) in the British Columbia subregions of the temperate rainforests of western North America. Data from Soil Landscape of Canada (v 2.2; Centre for Land and Biological Resources Research, 1996). c. Soil suborders in the Gulf of Alaska Coast subregion of the coastal temperate rainforests of western North America. Data from Soil Survey Staff (2012).

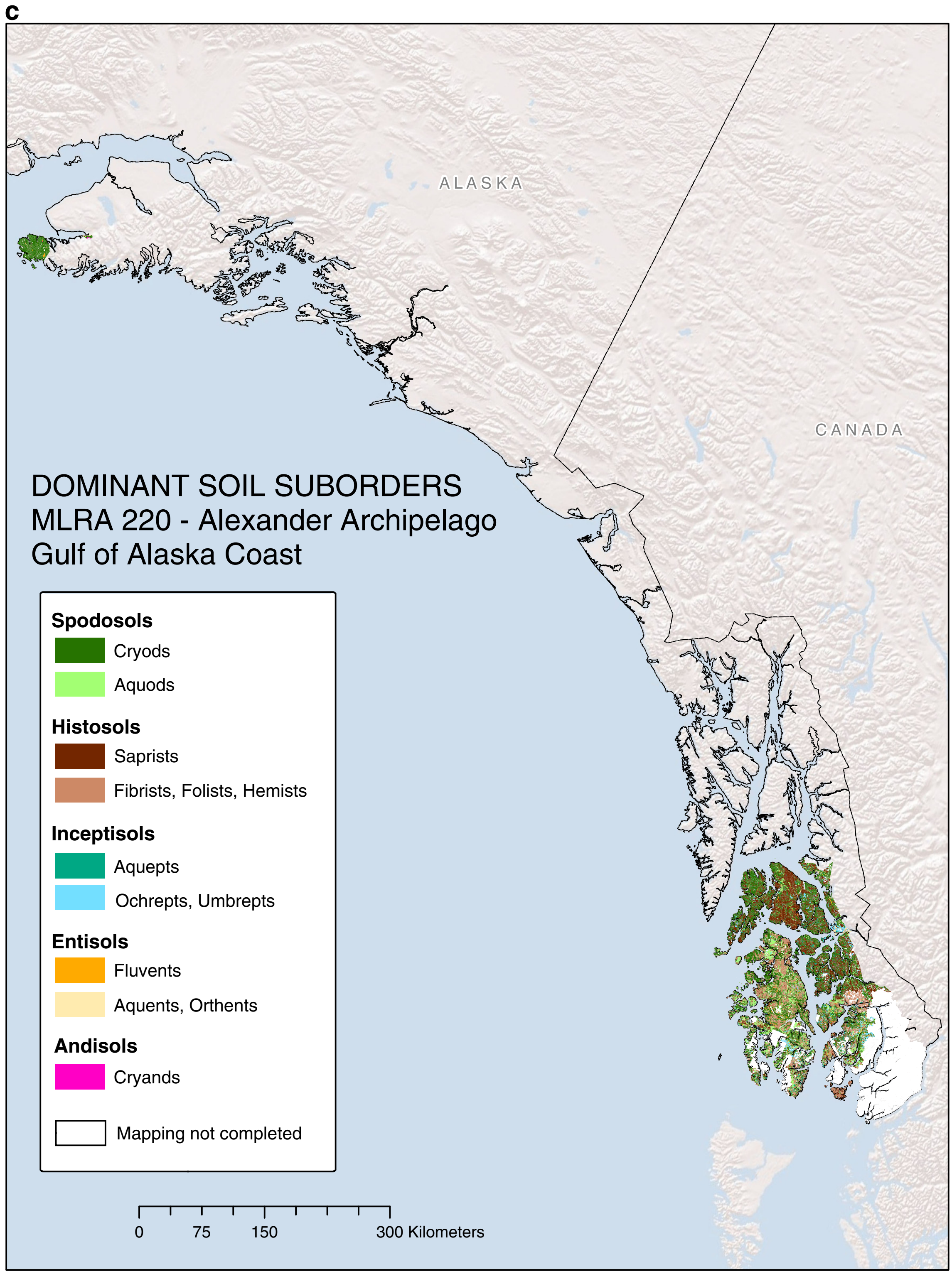

Fig. 2 (*continued*).

zones and World Reference Base soil groups at a global scale, Minasny et al. (2010) suggest that areas with moderate temperatures and precipitation regimes have greater pedodiversity and taxonomic differentiation, but our findings indicate that a region with moderate temperatures and high levels of precipitation can also have highly diverse soils.

One feature of pedodiversity is soil endemism. Bockheim (2005) identified endemic soils on the basis of having a centralized distribution, lacking competing soil series, and being unique to a particular area. Based on these criteria, 26% of the 482 soil series are endemic to temperate rainforests of the western US (listed in Supplement S2). The proportion of endemic soils varies by latitude (Fig. 5), and accordingly by mean

Fig. 3. Examples of soils in coastal temperate rainforest of western North America, including (A) a sandy, mixed, isomesic, ortstein, shallow Typic Duraquods (Blacklock soil series) on a 120 ka terraces along the Oregon coast, (B) a Typic Palehumults (Cunniff soil series) on an older uplifted marine terraces along the southern Oregon coast, (C) a Humo-Ferric Podzol (Haplorthods) in coastal British Columbia (Paul Sanborn photo), and (D a Lithic Humicryods from Port Graham, Alaska.
NRCS photo.

annual precipitation and temperature, with the greatest proportion of endemic soils occurring in the Coastal Redwood Belt (42% of soil series) and the least along the Gulf of Alaska Coast (5%). The reason for the lower pedodiversity along the Gulf of Alaska may relate to the young age of these soils and the uniformly cool, wet conditions of forests that are restricted to a narrow strip along the coast at these latitudes.

The range of parent materials, topography, mesoclimates, and pedogenic histories that are found in NAPC rainforests are all likely to contribute to the regional pedodiversity and soil endemism. Pedodiversity in the Pacific temperate rainforests may be enhanced by episodic tephra deposition (Briggs et al., 2006) and the variation in ages of landscapes from glacial recession (Bormann and Sidle, 1990; Crocker and Dickson, 1957; Ugolini, 1968) and exposure of raised beaches (Bockheim et al., 1996; Singleton and Lavkulich, 1987). Soil parent materials in southeastern AK, coastal BC, and northern WA were deposited during the last glacial period 13–16,000 yr BP (Mann and Hamilton, 1995), while soil parent materials in northern CA and southern OR can be hundreds of thousands of years old (Bockheim et al., 1996; Merritts et al., 1991). Though the NAPC and other temperate rainforest regions have broadly similar temperature and precipitation regimes from a global perspective, they still contain considerable climatic heterogeneity (Table 2; Alaback, 1991; Lawford et al., 1995). Subregion-scale differences in climate are further modified by gradients of oceanic influence and the topographic complexity of the Pacific Coast Ranges, and this mesoclimatic variation can have a significant effect on soil formation (Briggs et al., 2006). We believe that further investigation is warranted to more fully understand the relationships between pedodiversity, climate, and other factors of soil formation in temperate rainforests and other bioregions.

5.2. Soil properties in temperate rainforests

5.2.1. Soil carbon

One of the most striking aspects of NAPC temperate rainforest soils is their propensity for storing large quantities of organic C. Median organic C storage in the soils that we examined (211 Mg/ha) falls within the range of median values (143–289 Mg/ha) reported in other studies in the region (Table 5), and is substantially higher than that reported for other regions of the United States (60–100 Mg/ha; Homann et al., 2007). The values reported in Table 5 are likely underestimates of actual SOC, as they generally do not include soil C from the >2 mm fraction of soils, which has been found contain up to 46% additional SOC in old-growth forests in the Pacific Northwest (Homann et al., 2004). Broad-scale studies of soil C in Pacific temperate rainforests consistently report higher SOC values than the estimate of Post et al. (1985) for cool temperate rainforest globally (154 Mg/ha; Table 5), as well as for wet tropical forests (132 Mg/ha). Our estimate is closer to Post et al.'s (1985) for warm and subtropical wet forests (226 Mg/ha), but still below that for boreal rainforests (288 Mg/ha). A number of life zones included in Post et al.'s (1985) dataset have small sample sizes and may not adequately capture intra-zone heterogeneity, but temperate rainforests are clearly among the top bioregions in terms of SOC.

Climate, vegetation dynamics, disturbance history, decomposition rates, soil development, and the quantity and quality of dead organic matter all play a role in SOC storage in temperate rainforests. High SOC concentrations are known to be associated with regions of low moisture deficit, as in NAPC rainforests (Homann et al., 2007). Mild temperatures and abundant precipitation create highly favorable conditions for biomass production by long-lived conifers (Waring and Franklin,

Table 4
Soil chemical properties for the upper 100 cm for pedons representative of temperate rainforests along the North American Pacific Coast. Data from National Cooperative Soil Survey (2013). Additional physical and chemical data can be found in Supplement 1.

Pedon no.	Subgroup	Location	pH	Exch. bases [kmol(+)/ha]	SOC [Mg/ha]	Total N [kg/ha]	C:N ratio
80P0452	Mollic Hapludalfs	Mendocino, CA	5.9	–	–	–	–
80P0445	Ultic Hapludalf	Mendocino, CA	5.4	639	112	6178	18.1
80P0449	Ultic Haplustalf	Mendocino, CA	5.5	2035	88	6557	13.5
84P0900	Alic Fulvudand	Lincoln, OR	4.8	123	435	25,680	16.9
72C0055	Typic Fulvudand	Douglas, OR	5.2	335	518	27,014	19.2
84P0905	Typic Fulvudand	Grays Harbor, WA	4.7	168	793	39,241	20.2
78P0393	Typic Fulvudand	Grays Harbor, WA	5.0	–	–	–	–
98P0536	Pachic Fulvudand	Grays Harbor, WA	4.3	31	205	9135	22.4
82P0545	Lithic Cryofolist	Wrangell-Petersburg, AK	3.9	–	–	–	–
83P0826	Lithic Cryosaprist	Ketchikan, AK	6.3	–	1050	44,385	–
40A0647	Lithic Cryosaprist	Wales, AK	3.9	–	–	–	–
84P0141	Terric Cryosaprist	Ketchikan, AK	4.8	78	450	23,552	19.1
40A2989	Typic Dystrochrept	San Mateo, CA	5.9	–	35	–	–
01N1071	Andic Dystrudept	Tillamook, OR	5.2	203	455	32,042	14.2
72C0057	Andic Humudept	Coos, OR	5.2	1256	163	13,242	12.3
74C0145	Typic Humudept	Coos, OR	5.5	256	284	21,814	13.0
90P0072	Histic Placic Petraquept	Grays Harbor, WA	5.3	–	–	–	–
74C0148	Typic Duraquod	Coos, OR	4.7	96	217	9199	23.6
74C0147	Typic Haplorthod	Coos, OR	5.2	88	194	11,248	17.2
74C0149	Typic Haplorthod	Coos, OR	5.2	229	235	16,985	13.8
82P0618	Lithic Humicryod	Haines, AK	4.5	91	163	7384	22.1
82P0547	Lithic Humicryod	Wrangell-Petersburg, AK	3.8	–	–	–	–
82P0617	Typic Humicryod	Haines, AK	4.9	161	217	–	–
40A0623	Typic Humicryod	Prince of Wales, AK	4.4	19	154	5089	30.2
83P0072	Typic Humicryod	Wrangell-Petersburg, AK	4.6	–	–	–	–
92P1058	Typic Haplohumult	Curry, OR	5.0	101	116	–	–
40A3077	Typic Haplustult	Sonoma, CA	6.0	634	51	–	–
Minimum			3.8	19	35	5089	12.3
25th percentile			4.6	89	116	7384	13.8
Median			5.0	165	211	15,113	18.1
Mean			5.0	363	297	18,672	18.4
75th percentile			5.3	315	439	26,013	21.2
Maximum			6.3	2035	1050	44,385	30.2

1979), while cool, moist climate through much of the year results in low decomposition rates under the oxygen-limited conditions of wet soils (Schuur et al., 2001). Sun et al. (2004) suggest that high SOC levels in coastal OR may be caused by abundant precipitation increasing microbial activity and decomposition in the forest floor, where oxygen is rarely limiting, while retarding decomposition in the more poorly aerated mineral soil. Restricted drainage resulting from podsolization and paludification can lead to the development of thick, C-dense, organic layers, particularly in more northern NAPC rainforests. Even when podsolization does not lead to water-logged conditions, the translocation of Fe and Al can play an important role in SOC stabilization in the mineral layers of temperate rainforest Spodosols by forming organometallic complexes, among other mechanisms (Grand and Lavkulich, 2012).

The accumulation of SOC is an important component of total ecosystem C storage, which is exceptionally high in temperate rainforests, even more so than SOC alone (Keith et al., 2009; Smithwick et al., 2002). In western OR and WA, total ecosystem C has been found to strongly correlate with SOC <2 mm in the upper 20 cm of mineral soil (Homann et al., 2005). However, the mechanisms and duration of net SOC accumulation during ecosystem development are not always clear. Bormann et al. (1995) found no evidence of SOC reaching equilibrium over a 350 year chronosequence in southeast AK, but for forests in western OR, SOC content appears to reach an asymptote 150 to 200 years after stand initiation (Sun et al., 2004). Differences in disturbance type and severity, as well as climate, likely play a role. Several studies have documented the importance of windthrow in soil C dynamics, as the uprooting of trees disrupts podsolization and redistributes organic matter within a soil profile, with potentially positive effects for forest productivity (Bormann et al., 1995; Kramer et al., 2004). Soil chronosequences also show rapid accumulation of SOC in temperate rainforests undergoing primary succession (Bockheim et al., 1996; Burt and Alexander, 1996; Singleton and Lavkulich, 1987).

Though SOC levels were generally high, we also found considerable variability among soils in NAPC rainforests, which may reflect the high pedodiversity and varied soil development processes in the region. The IQR of SOC was considerably larger in our sample of temperate rainforest soils compared to other regional studies and estimates for rainforests globally (Table 5). Our sample was designed to capture the full range of soil types in the bioregion, while the others are more restricted. The distribution of SOC in the pedons that we examined was notably right-skewed, with a modal value of ~200 Mg/ha, and a small number of soils containing exceptionally large amounts of carbon (Fig. 5). A similar distributional pattern was noted by Post et al. (1982), and may be a common feature of SOC distributions at broad scales, in which case standard summary statistics of untransformed SOC data (e.g. mean and standard deviation) may be misleading.

There was a notable increase in SOC content, and particularly concentration (i.e. % SOC) with latitude within NAPC rainforests. The soils that we found with the lowest SOC were Haplustults, Haplohumults, and Hapludalfs in CA and southern OR, where summer moisture deficits are the highest in the region. In contrast, the abundant SOC in coastal BC and southeastern AK soils can be attributed to the gentle relief, slow rates of decomposition, and a high water table. Paludification is an important soil development process in this area. Translocated Fe and Al accumulates to form placic horizons, restricting drainage, raising the water table, and allowing C-rich organic horizons to form, often leading to the conversion of ecosystems from forests to bogs (Klinger, 1996; Turunen and Turunen, 2003; Ugolini and Mann, 1979).

Several other factors have been associated with SOC variation at smaller scales in NAPC temperate rainforests. SOC is positively associated with soil water holding capacity, coarse woody debris, and clay content (Homann et al., 2004, 2007). Vegetation and forest type have been observed to correlate with SOC (Edmonds and Chappell, 1994), as has parent material, with higher soil C concentration found on sedimentary

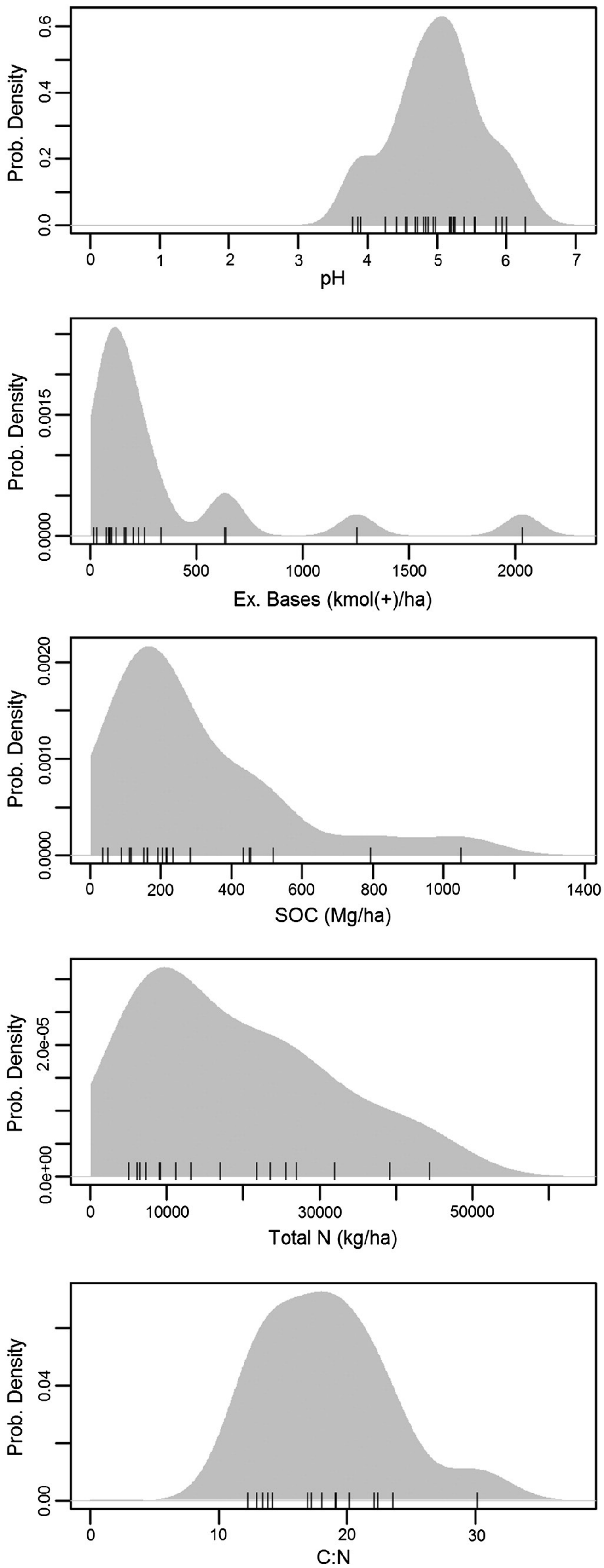

Fig. 4. Distribution of soil chemical properties among representative pedons in North American coastal temperate rainforests. Individual observations are displayed as ticks, while the probability density was generated using a kern density function in the R statistical environment.

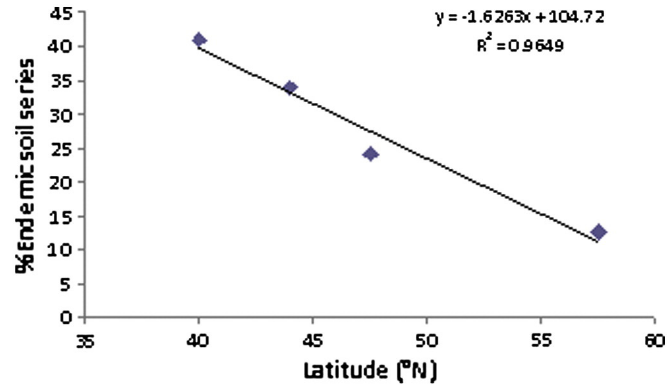

Fig. 5. Relationship between the proportion of endemic soil series and latitude in coastal temperate rainforests of western North America.

rock in the Pacific Northwest (Littke et al., 2011). Heterogeneity in SOC can be influenced by topography and hydrology, particularly in the forest–peatland complexes of coastal BC and AK, where C dynamics can be highly variable and soil properties are not necessarily directly coupled with vegetation (D'Amore et al., 2010; Hartshorn et al., 2003).

5.2.2. Soil nitrogen and carbon to nitrogen ratio

As with SOC, total soil N pools tend to be large in temperate rainforests of the NAPC, though they are also highly variable. Median total N in the pedons that we examined (15,113 kg/ha) is similar to values reported by Perakis and Sinkhorn (2011) and Smithwick et al. (2002) and higher than that reported by Edmonds and Chappell (1994) and Littke et al. (2011; Table 5). The levels of soil N that we found are higher than has been reported globally for temperate rainforests and for most other bioregions, with the exception of warm temperate and subtropical wet forests and rain tundra (Post et al., 1985; Table 5). We also found considerable variability in soil N (IQR: 7384–26,013 kg/ha), more so than in other studies (Table 5). Like SOC, soil N exhibits a right-skewed distribution, but with a much fatter tail; modal soil N is ~10,000 kg/ha, but seven of sixteen in pedons that we examined had N over 20,000 kg/ha (Fig. 5). NAPC rainforest soils with higher N concentration and content tend to be from the Andisol and Histisol orders, while those with lower N were often Alfisols and Spodosols, though a small sample size makes these observations tentative.

Soil N tends to be positively correlated with precipitation and clay content, though in the Pacific Northwest silt content appears to be more important than clay (Homann et al., 2007).

Studies on the OR Coast Range show great heterogeneity in N availability, with at least some forests that are N-saturated (Perakis and Sinkhorn, 2011; Perakis et al., 2011).

Nitrogen-fixing tree species, particularly *Alnus* spp., play an important role in N dynamics, nutrient uptake, and forest productivity during both primary succession (Bormann and Sidle, 1990) and in secondary forests, where red alder fixes significant amounts of N (Compton et al., 2003; Perakis et al., 2011).

Nitrogen immobilization in vegetation, soil microbes, and in O and Bh horizons are considered high in these ecosystems (Bormann and Sidle, 1990; Bormann et al., 1995).

In older soils, labile forms of N may become deficient in temperate rainforests, as in 120,000 year-old end members of a soil chronosequence in New Zealand (Menge et al., 2011).

^{15}N isotope studies show that important processes in bioavailable N-cycling in temperate rainforests (volcanic soils) include heterotrophic production of inorganic N, N immobilization by microbes, and leaching loss of organic N, rather than inorganic N (Huygens et al., 2008).

Table 5
Organic carbon and total nitrogen stores in soils of temperate rainforests in western North America.

Location	SOC [Mg/ha]	Total N [kg/ha]	C/N ratio	No. of sites (no. of pedons)	Unit of analysis	Reference
Coastal Oregon, Washington, northern California, & southeastern Alaska	211 (116–439)	15,113 (7384–26,013)	18.4 (13.8–21.2)	SOC: 20 (20) N, C/N: 16 (16)	Soil pedons throughout the US coastal temperate rainforests	This study and National Cooperative Soil Survey (2013)
Pacific Northwest (western OR, WA, southern BC)	143 (71–201)*	9141 (4726–14,020)*	17 (15–19)*	60 (60)	Douglas-fir plantations grouped by soil nutrient regimes (3) and parent material (3)	Littke et al. (2011)
Coastal Oregon & Washington	223 (124–309)*	11,710 (5642–15,220)*	20.3 (19.3–23.5)*	53 (53)	Second-growth Douglas-fir and western hemlock stands, grouped by forest type and subregion (5)	Edmonds and Chappell (1994)
Coastal Oregon & Washington	289 (210–362)	16,000 (NA)	16.6 (NA)	15 (31)	Mature western hemlock-Sitka spruce stands in (15) at two locations.	Remillard (1999) and Smithwick et al. (2002)
Coastal Oregon	268 (211–297)	15,890 (14.360–18,760)	16.7 (14.4–17.9)	10 (40)	Second-growth Douglas-fir stands (9) with Andisc soil properties on sandstone parent material	Sinkhorn (2007) and Perakis and Sinkhorn (2011)
Coastal southeastern Alaska	194 (157–216)*	NA	NA	3 (434)	Western hemlock-Sitka spruce stands in watersheds (3) with different disturbance histories	Kramer et al. (2004)
Cool temperate rainforests	154 (136–199)	11,490 (8595–13,630)	15.3 (13.6–17.0)	SOC: 17 N, C/N: 14	Holdridge terrestrial Life-zones of the world; samples from various sources; naturally vegetated sites	Post et al. (1985), Zinke et al. (1998)
Warm temperate/subtropical wet forests	226 (187–293)	16,980 (13,120–19,840)	14.7 (12.1–17.2)	SOC: 53 N, C/N: 52		
Tropical wet forests	132 (79–196)	6320 (4562–8555)	28.0 (20.5–39.1)	SOC: 23 N, C/N: 14		
Boreal rainforests	288 (147–349)	11,440 (4140–14,110)	25.8 (19.1–28.8)	SOC: 23 N, C/N: 21		

All values are unit of analysis medians, with interquartile ranges (25th–75th percentiles) in parentheses, except where data from individual sites were not available (denoted by *). Parentheses contain full range of values across all units of analysis. Where necessary and possible, reported values are based only on data from coastal rainforest portions of larger regions.

Tight N coupling in temperate rainforests results from "fierce" competition for bioavailable N by abiotic processes, soil microbes, and plant roots (Huygens et al., 2008).

It is generally assumed that ecosystem N is derived from atmospheric fixation, but recent work has shown bedrock as a potential source of soil N (Morford et al., 2011) and this may be the case in NAPC rainforests, where sedimentary parent materials have been correlated with higher soil N (Littke et al., 2011).

Typical C:N ratios in Pacific temperate rainforest soils appear to be around 18, based on our analysis and that of others (Table 5; Homann et al., 2007). This is higher than has been reported for temperate rainforests globally, and is higher than in other regions of the US and in most of the world's bioregions, with the exception of wet tropical forests, boreal rainforests, and tundra (Homann et al., 2007; Post et al., 1985; Table 5). Thus, while both SOC and soil N are high in NAPC temperate rainforests, high C:N ratios imply that SOC levels are generally more exceptional. The representative pedons that we examined have C:N ratios with an approximately normal distribution, and though they were more variable than demonstrated by other studies in the region (Table 5), such variability does not appear to be atypical of bioregions globally (Post et al., 1985). High C:N ratios are associated with high levels of precipitation and lower temperatures, decomposition rates, silt and clay content, and litter quality, the latter being prevalent in coniferous forests (Homann et al., 2007; Post et al., 1985). In the Pacific Northwest, glacial parent material also tends to be correlated with higher C:N ratios (Littke et al., 2011).

5.2.3. Other soil properties and characteristics

Soils in NAPC temperate rainforests are moderately deep, well-drained, have abundant weatherable minerals (based on mineral classes), are not subject to deep freezing, and are able to hold abundant moisture. Pacific temperate rainforests also tend to have low bulk density, moderate and variable CEC, and be fairly acidic. Low soil pH is particularly prevalent at higher latitudes where Spodosols are common (Table 4) and Al-saturation is also high. By contrast, base saturation and exchangeable cation concentrations and contents, which are low overall, tend to be higher in the southern portions of the region, where Alfisols are more common. There are numerous pedogenic factors and processes that influence soil properties in NAPC rainforests, and we highlight just a few here.

The supply of soil nutrients, particularly base cations, is influenced by marine inputs and parent materials in NAPC rainforests. Soil parent materials can influence nutrient availability in temperate rainforest soils (e.g. Kranabetter and Banner, 2000; Littke et al., 2011), but differences among surface layers are not necessarily large and can diminish over time (Heilman and Gass, 1974; Kranabetter and Banner, 2000). Studies in coastal OR have found that marine aerosols are the primary source of Ca, Mg, and K for many forests, particularly those where local rates of weathering and fresh mineral inputs are constrained (Bockheim and Langley-Turnbaugh, 1997; Compton et al., 2003; Perakis et al., 2006). These investigations also indicate that net cation loss is primarily controlled by the leaching of nitrate and organic anions.

The progression of soils from Inceptisols to Spodosols, and accompanying changes in soil properties, is common throughout the entire NAPC region. This process typically involves redistribution and transformation of Fe and Al, loss of base cations, and buildup of organic matter. Accumulating organic matter leads to soils with high ECEC, extractable acidity, and 1500 kPa water-holding capacity, and later, declining soil pH and increasing extractable Fe, especially organic and amorphous forms. Such a progression has been observed in chronosequences in southwestern OR (Bockheim et al., 1996), coastal BC (Singleton and Lavkulich, 1987), and southeastern AK (Burt and Alexander, 1996). In the southern portion of the NAPC, this process is often accompanied by desilication, and leads to the development of clay-enriched Spodosols and Ultisols (Bockheim et al., 1996; Langley-Turnbaugh and Bockheim, 1998). In the north, podsolization commonly involves the development of a drainage-restricting hardpan layers, potentially leading to paludification (Klinger, 1996; Ugolini and Mann, 1979).

5.3. The role of soils in temperate and tropical rainforest ecosystems

Rainforests generally have high productivity and aboveground biomass, and tall, multilayered canopies. Tropical and temperate rainforests differ in global coverage (12% vs. 2%), local tree species richness (>50 vs. <20), dead organic matter accumulations (low vs. high), and tree lifespans (50–100 vs. 400–1500 yrs; DellaSala et al., 2011; Waring and Franklin, 1979). Likewise, there are similarities and differences in the soils of tropical and temperate rainforests. Soils in both bioregions are moderately deep to deep, have high total N storage, and tend to be acidic and Al-saturated (Table 6). Whereas the soil temperature and moisture regimes are isomesic and udic in temperate rainforests, they are isohyperthermic (mean annual soil temperature ≥22 °C and difference between mean summer and winter temperatures <6 °C) and perudic in tropical rainforests.

Soils in coastal temperate rainforests tend to be young (<500 ka) and less weathered, while those in tropical rainforests commonly are of early Quaternary to late Tertiary age (>1500 ka) and contain low levels of weatherable minerals, low CEC, and narrow CEC7/clay ratios (Table 6). Whereas the dominant soil-mineral classes are mixed, ferrihydritic, and isotic in soils of temperate rainforests, they are kaolinitic, ferruginous (abundant Fe_2O_3), or parasesquic (abundant gibbsite and Fe_2O_3) in soils of tropical rainforests. Soils of both regions tend to be Al-saturated.

A major difference in soils of temperate and tropical rainforest is the storage of SOC. The representative temperate rainforest pedons considered in this study contain a median of 211 Mg/ha, while the tropical rainforest soils from Micronesia contain less, at 162 Mg/ha (Table 6). Temperate rainforest soils also have substantially higher C:N ratios than their tropical counterparts (MD: 18.1 v. 10.4). Base cation pools are just slightly higher in temperate than tropical rainforest soils, which contain medians of 165 and 129 $kmol_c$/ha, respectively. The profile storage of total N is high in both bioregions (MD: 15,113 and 15,980 kg N/ha respectively), though it appears to be more variable in temperate areas, where rainforests can be N-limited or N-saturated (Table 6; Perakis et al., 2006). The abundance of N in tropical rainforest soils was described as the "nitrogen paradox" by Hedin et al. (2009), in which this buildup of N does not impact plant physiology and biodiversity. Similar phenomena may be applicable in N-saturated temperate rainforests (Perakis and Sinkhorn, 2011).

The NRCS databases lacked information about plant-available P. Based on the abundance of Spodosols, Andisols, and Histosols, which readily fix P, we suspect that P may often be limiting in temperate rainforests. Evidence in support of this has come from studies on Vancouver Island that indicates that forest productivity is co-limited by P and N (Blevins et al., 2006; Kranabetter et al., 2005). Richardson et al. (2004) found that P limitation developed in the older soils of a glacial chronosequence in temperate rainforests in New Zealand. Tropical rainforests are also subject to P deficiencies due to the tight nutrient cycling of that element (Hedin et al., 2009).

These comparisons suggest that soils in temperate rainforests generally are somewhat more fertile than those in tropical rainforests. The storage of nutrients is comparable in some respects, such as large total soil N capacity, but different in others, like SOC and cation-exchange capacity. Of course, forest fertility in these ecosystems is not solely a function of their soils, but also of how nutrients are cycled through their soils.

Both tropical and temperate rainforests utilize biogeochemical pathways that are absent or insignificant in most other ecosystems. A humid climate and tall canopies allow these forests to capture significant quantities of water and nutrients from cloud deposition (Clark et al., 1998; Weathers et al., 2000). Rainforests generally contain abundant epiphytes that both benefit from and enhance cloud–water interception (Coxson and Nadkarni, 1995). Litter and other detritus that collect in rainforest canopies are sufficient to form arboreal Histosols (Enloe et al., 2006). In both types of rainforest, fine roots tend to be concentrated in the topsoil and forest floor, contributing to rapid turnover of organic matter and enabling "direct" nutrient cycling (Stark and Jordan, 1978; Vogt et al., 1983). A substantial proportion of nutrients are immobilized in aboveground biomass in at least some temperate and tropical rainforests (Bormann and Sidle, 1990; Edwards and Grubb, 1982). In temperate rainforests, large accumulations of woody detritus and forest floor biomass can also act as large stores of nutrients, but in tropical areas, rainforests have much higher rates of decomposition and thus smaller dead organic matter pools (Chambers et al., 2000; Vogt et al., 1986).

A major difference in biogeochemical cycling among rainforests is the high rates of nutrient exchange with marine ecosystems in many temperate regions, but few tropical regions. Tropical rainforests commonly occur inland from oceans, whereas nearly all temperate rainforests are on or near coastlines. In the NAPC region, this allows migrating salmon to bring substantial quantities of nutrients, particularly N and P, from the ocean into forest ecosystems (Gende et al., 2002; Naiman et al., 2002), while marine aerosols can provide significant inputs of K, Ca, and Mg (Bockheim and Langley-Turnbaugh, 1997; Perakis et al., 2006).

Tropical and temperate coastal rainforests have some similar soil-forming processes, including base-cation leaching, melanization, and gleization. However, the major difference between these two bioregions is that whereas podsolization is a dominant soil-forming process in temperate rainforests, ferrallitization is of key importance in tropical rainforests. In temperate rainforests the environmental conditions create strongly acid soil solutions that enable the complexation of Al, whereas the lesser acidity of leachates in tropical rainforests enables rapid hydroxylation and the formation of Al intergrade minerals (Righi et al., 1990).

Table 6
Comparison of typical soil characteristics in tropical and temperate rainforests. Quantities represent typical ranges or medians with interquartile ranges in parentheses. For temperate rainforests, characteristics are derived from Table 2 and the 27 representative pedons of North American Pacific coastal rainforests (Table 4, Supplement S1). For tropical rainforests, characteristics are summarized from the soil series in the Perox suborder from Micronesia in the Pacific Basin.
National Cooperative Soil Survey (2013) and Soil Survey Staff (2013c).

Property	Temperate rainforests	Tropical rainforests
Soil depth [cm]	86–150	>100
Weatherable minerals [%]	>10	<10
Age [ka BP]	<500	>1500
Soil temperature regime	Isomesic, isofrigid	Isohyperthermic
Soil moisture regime	Udic, some aquic	Perudic
Cation-exchange capacity [cmol(+)/kg]	33 (17–42)	6 (4–10)
Effective CEC [cmol(+)/kg]	<2–<15	<1–<10
CEC7:clay Ratio	1–6	<1
Al saturation [%]	32–78	44–74
pH	4.6–5.3	3.9–6.3
Total base-cation storage to 1 m [kmol(+)/ha]	165 (89–315)	129 (100–236)
Soil organic C storage to 1 m [kg/ha]	211 (116–439)	162 (101–194)
Total N storage to 1 m [kg/ha]	15,113 (7384–26,013)	15,980 (14,312–18,172)
C:N ratio	18.1 (13.8–21.2)	10.4 (7.6–11.3)

6. Conclusions

To investigate the characteristics of temperate rainforest soils we delineated the soils in North American Pacific coastal temperate rainforests as a case study, assessed their diversity and properties, and compared them and their role in rainforest ecosystems with their tropical counterparts. We draw the following conclusions:

- Soils of the NAPC temperate rainforest are exceptionally diverse, including 8 orders and 31 suborders, owing to significant heterogeneity in soil-forming factors. There are also a large number of endemic soils in the region, constituting approximately 26% of described soil series. Within the region, pedodiversity and the proportion of endemic soils is inversely related to latitude.
- Soils of NAPC temperate rainforests are deep, hold abundant moisture, are not subject to deep-freezing, and have abundant weatherable minerals and a moderately high cation-exchange capacity. These soils also tend to be acidic, Al-saturated and enriched in extractable Fe and Al. Organic C and total N contents and C:N ratios are high overall, but SOC and N are also quite variable, with right-skewed, long-tailed distributions. Levels of base cations are somewhat low, also with a right-skewed long-tailed distribution.
- Soils in temperate rainforests share some characteristics with tropical rainforest, while differing in others. Both temperate and tropical rainforest soils tend to be deep, acidic, and Al-saturated, and can have high levels of N, and deficiency in P. Soils in temperate rainforests are generally younger and somewhat more fertile, with different and more abundant weatherable minerals. They also have higher C storage, C:N ratios, and cation exchange capacity than tropical rainforest soils.

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